

# Pronouns reactivate conceptual representations in human hippocampal neurons

D. E. Dijksterhuis<sup>1\*†</sup>, M. W. Self<sup>1\*</sup>, J. K. Possel<sup>1</sup>, J. C. Peters<sup>1,2</sup>, E.C.W. van Straaten<sup>3</sup>, S. Idema<sup>3</sup>, J. C. Baaijen<sup>3</sup>, S. M. A. van der Salm<sup>4</sup>, E.J. Aarnoutse<sup>4</sup>, N. C. E. van Klink<sup>4</sup>, P. van Eijsden<sup>4</sup>, S. Hanslmayr<sup>5</sup>, R. Chelvarajah<sup>6,7</sup>, F. Roux<sup>7</sup>, L. D. Kolibius<sup>5,8</sup>, V. Sawlani<sup>6,7</sup>, D. T. Rollings<sup>6</sup>, S. Dehaene<sup>9,10</sup>, P. R. Roelfsema<sup>1,11-13†</sup>

## Affiliations:

<sup>1</sup>Vision and Cognition, Netherlands Institute for Neuroscience, Amsterdam, Netherlands

<sup>2</sup>Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, Maastricht, Netherlands

<sup>3</sup>Department of Neurosurgery, Amsterdam University Medical Centre location VUmc, Amsterdam, Netherlands

<sup>4</sup>Department of Neurology and Surgery, University Medical Centre Utrecht, Utrecht, Netherlands

<sup>5</sup>Centre for Cognitive Neuroimaging, School of Psychology and Neuroscience, University of Glasgow, Glasgow, United Kingdom

<sup>6</sup>Complex epilepsy and surgery service, Queen Elizabeth Hospital, Birmingham, United Kingdom

<sup>7</sup>School of Psychology, University of Birmingham, Birmingham, United Kingdom

<sup>8</sup>Columbia University, Department of Biomedical Engineering, USA

<sup>9</sup>Université Paris Saclay, INSERM, CEA, Cognitive Neuroimaging Unit, NeuroSpin center, Saclay, France

<sup>10</sup>Collège de France, Paris, France

<sup>11</sup>Department of Integrative Neurophysiology, VU University, Amsterdam, Netherlands.

<sup>12</sup>Department of Neurosurgery, Amsterdam University Medical Centre, Amsterdam, Netherlands.

<sup>13</sup>Laboratory of Visual Brain Therapy, Sorbonne Université, Institut National de la Santé et de la Recherche Médicale, Centre National de la Recherche Scientifique, Institut de la Vision, Paris, France

\* These authors contributed equally to this work

† Corresponding authors: [dorisdijk@gmail.com](mailto:dorisdijk@gmail.com); [p.roelfsema@nin.knaw.nl](mailto:p.roelfsema@nin.knaw.nl)

**One-Sentence Summary:** Pronouns activate neurons in the human hippocampus if they refer to the concepts to which the cells are tuned.

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## ABSTRACT

1 **During discourse comprehension, every new word adds to an evolving representation of**  
2 **meaning that accumulates over consecutive sentences and constrains the next words. To**  
3 **minimize repetition and utterance length, languages use pronouns, like the word ‘she’, to**  
4 **refer to nouns and phrases that were previously introduced. It has been suggested that**  
5 **language comprehension requires that pronouns activate the same neuronal represen-**  
6 **tations as the nouns themselves. Here, we test this hypothesis by recording from**  
7 **individual neurons in the human hippocampus during a reading task. We found that cells**  
8 **that are selective to a particular noun are later reactivated by pronouns that refer to the**  
9 **cells’ preferred noun. These results imply that concept cells contribute to a rapid and**  
10 **dynamic semantic memory network which is recruited during language comprehension.**  
11 **This study uniquely demonstrates, at the single-cell level, how memory and language are**  
12 **linked.**

13 Consider these two sentences: “John and Mary walked into a bar. He sat down at a table.”.  
14 When we read the pronoun ‘he’, we realize that John, the only male character in the story, must  
15 be the person who sat down at a table. In linguistic terms, John is the ‘antecedent’ of the  
16 pronoun. This example illustrates how a narrative activates successive concepts in our brain,  
17 including their interrelations, allowing us to incrementally build up a conceptual representation  
18 of the discourse<sup>1-3</sup>. Previous brain-imaging studies have gained insight into the brain regions  
19 that activate during sentence and discourse comprehension<sup>4-11</sup>. However, the resolution of  
20 these non-invasive imaging methods does not suffice to track the neuronal assemblies that  
21 encode individual concepts in the human brain during reading.

22 In recent years, it has become possible to directly record the activity of single neurons in  
23 patients who are implanted with electrodes to locate the source of their epilepsy<sup>12,13</sup>. These  
24 studies demonstrated the existence of ‘concept cells’ in the medial temporal lobe<sup>14-16</sup>. Concept

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25 cells have an invariant and multimodal selective response to a concept. They contribute to the  
26 representation of meaning because they not only activate when the participant sees a picture of  
27 a specific individual for example, but also when the participant hears or reads the name of this  
28 person, or recalls this individual from memory<sup>14,17-19</sup>. We hypothesized that monitoring the  
29 activity of concept cells during reading could provide insight into the dynamics of semantic  
30 representations during language comprehension. In the present study, we illustrate the  
31 possibilities of this approach by examining how pronouns that are encountered during reading  
32 influence the neuronal representation of concepts that were introduced in an earlier sentence.  
33 Specifically, we asked if pronouns influence the activity of hippocampal neurons. Our results  
34 reveal that hippocampal cells respond robustly to preferred nouns and that they are specifically  
35 reactivated by a pronoun that refers to them as antecedent. The results represent the first  
36 measurements of the magnitude, latency and duration of hippocampal single cell responses to  
37 nouns and pronouns during reading, while participants incrementally build up a semantic  
38 representation of a narrative.

39 We recorded from patients with pharmacologically intractable epilepsy who were  
40 implanted with depth electrodes in the hippocampus, to localize seizure foci for clinical  
41 purposes. During an initial screening session, the patients viewed many pictures of celebrities  
42 and family members, and we identified pictures that, for a given neuron, elicited a significantly  
43 higher response than other pictures (Methods). We used the results of the screening session,  
44 aiming to select three nouns for the main reading task: one was the preferred person for a cell  
45 (the preferred noun) and two nouns referred to a male and a female that did not activate that  
46 cell (although the non-preferred nouns sometimes activated other, simultaneously recorded  
47 cells).

48 In the main task, on every trial, patients read two sentences which were presented as a  
49 stream of words on a computer screen (Fig. 1A and Table 1). The subjects of the first sentence

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50 were always two of the three selected nouns (e.g. Courtney Love and Barack Obama), and the  
51 second sentence started with a pronoun (either she or he). We then asked a question to verify  
52 that the patients understood the meaning of the sentences and maintained focus throughout the  
53 experiment. The mean accuracy was  $89 \pm 2\%$  (s.e.m), significantly higher than the chance level  
54 of 33% (Wilcoxon signed rank test,  $p = 1.2 \cdot 10^{-4}$ ; Methods and Fig. 1B).

55 We identified a total of 529 single and multi-units in the hippocampus of 22 participants  
56 (see Table S3 and Methods). We selected cells for further analyses based on their response  
57 during the reading task, in which 307 cells responded to the nouns. We focused our analysis  
58 on 53 noun-selective cells (recorded in 14 of the participants), which responded significantly  
59 stronger to a preferred noun than to the other two nouns ( $p < 0.05$ , permutation-based Poisson  
60 ANOVA and post-hoc Poisson t-test, see Methods) (Fig. 1C). Of the noun-selective cells, we  
61 defined 19 to be concept cells, because they preferred the same concept as a picture in the  
62 screening task and as a word during the reading task (Methods, Fig. S1 and Table S2; we note  
63 that a previous study included more extensive tests of multimodality<sup>20</sup>). The remaining 34 cells  
64 were noun-selective, but either did not respond to pictures or preferred a different concept  
65 during the screening task, and we will refer to them as noun-selective, non-concept cells  
66 (NSNCs). Figure 1D illustrates the activity of an example concept cell that responded  
67 selectively to a picture of the animated male movie character Shrek during the screening task.  
68 The cell also preferred the written noun ‘Shrek’ (Noun<sub>Pref</sub>) (Figure 1E), but it did not respond  
69 to Courtney Love and a male family member of the participant (Nouns<sub>NonPref</sub>). The pronoun ‘he’  
70 in the second sentence activated the cell if it referred to Shrek in the first sentence (Pronoun<sub>Ref</sub>).  
71 The pronoun ‘she’ referred to the other noun (Pronoun<sub>PresNotRef</sub>; Table 2 specifies the naming  
72 conventions) and did not activate the cell. Furthermore, ‘he’ also did not activate the cell if  
73 Shrek was absent from the first sentence (Pronoun<sub>AbsentSame</sub>). Hence, only pronouns referring to  
74 Shrek activated the neuron.

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75 To examine the generality of this effect, we carried out an analysis across the population  
76 of 53 noun-selective cells. We first examined the activity elicited by the nouns with a cross-  
77 validation approach. We used half of the trials to determine the preferred noun and the other  
78 half for the statistics. Across the population, the activity elicited by Noun<sub>Pref</sub> was  $5.4 \pm 0.5$  Hz  
79 (mean  $\pm$  s.e.m.), which was significantly higher than the activity of  $2.9 \pm 0.5$  Hz elicited by the  
80 other, non-preferred nouns (t-test,  $t = 3.9$ ,  $p = 3.0 \cdot 10^{-4}$ ). We determined the neurons' response  
81 latencies as the first of 10 subsequent time-bins where the response to Noun<sub>Pref</sub> was higher than  
82 the response to the other nouns ( $P < 0.05$ ; see Methods and Fig. 2D-F). Regardless of whether  
83 Noun<sub>Pref</sub> was presented at the first or second position in the first sentence, the cells activated  
84 on average  $210\text{ms} \pm 38\text{ms}$  (s.e.m.) after the presentation of the preferred noun.

85 We next examined the responses elicited by the pronouns. On average, pronouns referring  
86 to Noun<sub>Pref</sub> (Pronoun<sub>Ref</sub>) activated the hippocampal neurons more strongly than pronouns that  
87 did not (paired t-test,  $t_{52} = 6.8$ ,  $p = 3.3 \cdot 10^{-7}$ ) (Fig. 2A). This effect was significant for 25% of  
88 the noun-selective cells and for 42% of the concept cells (permutation-based Poisson ANOVA;  
89  $P < 0.05$ ). Interestingly, the responses of concept cells to Pronoun<sub>Ref</sub> ( $5.0 \pm 0.9$  Hz,  $N = 19$ )  
90 were stronger than those of the NSNC cells ( $2.3 \pm 0.5$  Hz,  $N = 34$ ; t-test corrected for unequal  
91 variance,  $t = 2.6$ ,  $p = 0.016$ ; Fig. 2A). The extra activity elicited by Pronoun<sub>Ref</sub> emerged  
92 gradually (Fig. 2G) with a latency of  $600\text{ms} \pm 110\text{ms}$ , which is longer than the latency of the  
93 response to Noun<sub>Pref</sub> ( $p = 0.010$ , bootstrapping test), although activity built up gradually so that  
94 the inclusion of more cells might have shortened the latency estimate. There were no significant  
95 differences in response magnitude (independent samples t-test,  $t_{51} = 0.19$ ,  $p = 0.85$ ) or latency  
96 ( $p = 0.54$ ; bootstrap test, see Methods) between the left and right hemispheres.

97 Is the response to Pronoun<sub>Ref</sub> caused by a prolonged activation by the preferred noun,  
98 extending into the second sentence? To examine this question, we selected the first sentences  
99 with Noun<sub>Pref</sub> and compared the activity elicited by pronouns that referred to Noun<sub>Pref</sub>

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100 (Pronoun<sub>Ref</sub>) and to the other noun (Pronoun<sub>PresNotRef</sub>); for example ‘Shrek and Courtney Love’  
101 followed by ‘He’ or ‘She’. The response elicited by Pronoun<sub>Ref</sub> was higher than that evoked by  
102 Pronoun<sub>PresNotRef</sub> (paired t-test,  $p = 1.4 \cdot 10^{-7}$ ) (Fig. 2B), indicating that it reflects the antecedent  
103 of the pronoun and is not a lingering memory trace of Noun<sub>Pref</sub>.

104 We next investigated whether the pronoun activation reflected tuning to gender rather than  
105 to the identity of the antecedent. We compared trials in which the pronoun referred to Noun<sub>Pref</sub>  
106 (e.g. ‘Shrek and Courtney Love’ followed by ‘He’) to trials in which the same pronoun referred  
107 to a different noun of the same gender (Pronoun<sub>AbsentSame</sub>, e.g. ‘Barack Obama and Courtney  
108 Love’ followed by ‘He’). Pronoun<sub>Ref</sub> elicited a higher response than Pronoun<sub>AbsentSame</sub> ( $N = 45$ ,  
109 paired t-test,  $p = 1.5 \cdot 10^{-3}$ ; Fig. 2C), implying that the pronoun responses reflected the identity  
110 of the antecedent and not the gender.

111 We examined whether population responses evoked by pronouns resembled those evoked  
112 by the nouns and how different cell groups contributed to the population response. To this end,  
113 we trained a linear support-vector machine (SVM) to discriminate between responses elicited  
114 by Noun<sub>Pref</sub> and Noun<sub>NonPref</sub>. We constructed 1,000 surrogate-populations by randomly  
115 choosing units from the noun-selective cells with replacement ( $N = 50$  cells; we excluded three  
116 cells from this analysis, Table S3). We trained the classifier on activity in the noun time-  
117 window and tested the classifiers on held-back trials in a series of sliding windows covering  
118 the two sentences. We split trials based on first sentences in which Noun<sub>Pref</sub> 1) appeared at the  
119 first position, 2) appeared at the second position and 3) was absent. The classifier output  
120 represents the fraction of trials in a particular time-window in which the neuronal responses  
121 are labelled as elicited by Noun<sub>Pref</sub> (y-axis in Fig. 3A). As expected, the classifier output  
122 increased shortly after the presentation of Noun<sub>Pref</sub> at both the first and second position,  
123 labelling the activity as evoked by Noun<sub>Pref</sub> in ~90% of trials (Fig. 3A). Interestingly, when  
124 Noun<sub>Pref</sub> was at the first position, the classifier output increased slightly after the presentation

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125 of the second, non-preferred noun (black arrow in Fig. 3A), which may reflect a mental process  
126 that relates the two nouns.

127 We next tested the classifier on the second sentence, on which it had not been trained. We  
128 compared the classifier output between trials in which the pronoun referred to the preferred  
129 noun (Pronoun<sub>Ref</sub>), trials on which it referred to the other noun (Pronoun<sub>PresNotRef</sub>) and trials on  
130 which Noun<sub>Ref</sub> was absent from the first sentence. The activity pattern elicited by Pronoun<sub>Ref</sub>  
131 was like that elicited by Noun<sub>Ref</sub>, causing a higher decoder output than on trials in which the  
132 pronoun referred to the other, non-preferred noun and on trials without Noun<sub>Ref</sub> in the first  
133 sentence (Fig. 3A). The decoder output was also higher than on trials in which the antecedent  
134 was the non-preferred noun with the same gender (Pronoun<sub>AbsentSame</sub>; Fig. S2A). We replicated  
135 the results with a cross-decoding analysis, training and testing on all combinations of time-bins  
136 in the two sentences. Cross-decoding worked in both directions, from noun to pronoun and  
137 from pronoun to noun (Fig. S2B).

138 To investigate which cells contributed most to the selectivity of the pronoun response, we  
139 built decoders by successively adding concept cells ( $N = 19$ ), NSNC cells ( $N = 19$  selected of  
140 a total of 31 units) and neurons that responded to nouns without significant tuning in different  
141 orders ('untuned',  $N = 215$ , noun response  $> 0.5$  Hz above baseline; see Table S3 for inclusion  
142 of cells) (Fig. 3B). Decoders built from noun-selective cells (concept and NSNC) to decode  
143 nouns also reliably decoded the pronoun of the second sentence, whereas adding untuned cells  
144 did not improve this form of generalization (Fig. 3C). Interestingly, adding NSNC cells to  
145 decoders that already included all concept-cells did not improve decoding, whereas adding  
146 concept-cells to decoders with only NSNC cells improved decoding accuracy ( $p = 0.015$ ,  $z$ -  
147 test) (Fig. 3B,C). These results indicate that decoding of the pronoun's antecedent relied mostly  
148 on the concept cells, with a smaller contribution from NSNC cells and little contribution from  
149 the untuned cells.

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150 Two additional observations demonstrated that the neural responses were linked to the  
151 subjects' interpretation of the pronoun on individual trials. First, we compared the response to  
152 pronouns that referred to the preferred noun (Pronoun<sub>Ref</sub>) between correct trials and error trials,  
153 on which the participants reported the incorrect noun in response to the question at the end of  
154 the trial. The hippocampal response was higher on correct trials than on error trials (t-test, two-  
155 tailed,  $t = -2.31$ ,  $p = 0.008$ ,  $N = 35$ ; Fig S3A), indicating that it predicted the participant's  
156 interpretation of the second sentence.

157 Second, we analysed ambiguous trials with two nouns of the same gender in the first  
158 sentence, so that they competed for a status as antecedent of the pronoun ('Shrek and Barack  
159 Obama went into a bar. He sat the table', followed by the question 'Who sat at the table?') (Fig.  
160 3D; Table 2). We predicted that the strength of the response to Noun<sub>Pref</sub> in the first sentence  
161 might relate to the probability that the participant chooses it as antecedent and reports it in  
162 response to the question. In accordance with this prediction, the decoder output for the  
163 preferred noun of the first sentence was stronger if the participant chose it in response to the  
164 question (Fig. 3D) ( $p = 0.045$ , z-test). Furthermore, decoder output also ramped up at the end  
165 of the second sentence if the participants chose the preferred noun (Fig. 3D). Hence, the activity  
166 of hippocampal neurons during reading is related to the strength of the conceptual  
167 representations and predicts the resolution of pronoun ambiguity.

168 The results, taken together, demonstrate a link between the activity of neurons in the human  
169 hippocampus and the incremental representation of concepts and their interrelations during  
170 sentence reading. Previous studies indicated how language understanding relies on the  
171 integration of semantic knowledge, to which the hippocampus contributes<sup>21-26</sup>, with linguistic  
172 representations<sup>27-31</sup>. We here provided the first measurements of single unit activity in the  
173 hippocampus during a task in which participants build up a semantic representation of a  
174 narrative<sup>32</sup>, in which a pronoun brings one of the characters into the foreground of thought.

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175 Interestingly, most of the information about the antecedent of the pronoun was carried by  
176 concept cells, which responded to a concept irrespective of whether it was presented as picture  
177 or noun, indicating that their activity disambiguates otherwise identical pronouns.

178 Hippocampal neurons responded to both their preferred noun and to pronouns referring to  
179 that noun. The hippocampal pronoun response could thereby link new information of the  
180 narrative to the appropriate concept. For example, when we read about Shrek that ‘he’ put on  
181 sunglasses, we can update Shrek’s representation and predict his future appearance<sup>14,33–35</sup>. In  
182 accordance with this view, damage to the hippocampus can lead to impairments in pronoun  
183 production and comprehension and patients with hippocampal lesions often fail to retrieve a  
184 pronoun’s antecedent<sup>36,37</sup>. Our results support a role for the hippocampus in pronoun resolution,  
185 because the pronoun response was weaker on error trials and hippocampal activity predicted  
186 the perceived antecedent of the pronoun on ambiguous trials.

187 The latency of the pronoun response was 600ms, which was longer than the latency of  
188 210ms of the noun response, and most likely reflects processes that link the representation of  
189 the pronoun in language areas to the appropriate concept in the hippocampus. The long latency  
190 is remarkable because pronouns are thought to increase discourse efficiency, allowing shorter  
191 utterances to activate the same concepts as longer noun phrases<sup>1,38</sup>. The present results indicate  
192 that this pronoun advantage may only occur for noun phrases that take several hundreds of  
193 milliseconds. We note, however, that the latency of the pronoun response in the hippocampus  
194 might be shorter if there is only a single possible antecedent.

195 Language theories propose that pronouns have additional advantages, such as signalling  
196 that the subject of the narrative remains the same across sentences<sup>39</sup>. Our results inform these  
197 theories<sup>1,39</sup>, including ‘prominence’ theories that propose that pronouns usually refer to the  
198 most prominent nouns of a discourse<sup>40</sup>. According to those theories, nouns that fulfil a similar  
199 role in previous sentences compete for selection based on their prominence, which reflects on

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200 how important they are in the narrative<sup>40</sup>. So far, these theories could only be tested  
201 indirectly<sup>41,42</sup>, short of a method to measure prominence in the brain. Our results on trials with  
202 two nouns of the same gender, which caused the pronoun to be ambiguous, provided insight  
203 into the neuronal underpinnings of prominence. On these ambiguous trials, the participant  
204 could report either noun as antecedent of the pronoun. When the participants reported that the  
205 pronoun referred to the preferred noun, the response to that noun was stronger during the first  
206 sentence, and hippocampal activity ramped up once more at the end of the second sentence.  
207 These results suggest that prominence is related to the strength of the conceptual  
208 representations, which depend, in part, on the activity of hippocampal neurons.

209 Theories about the evolving mental representation of the narrative during reading suggest  
210 that previously read words are stored in working memory so that they can be combined with  
211 new information<sup>28-30,32,43,44</sup>. Interestingly, the hippocampal activity elicited by nouns lasted  
212 only 300-400ms and was curtailed by later words, which has implications for the internal  
213 structure of these representations<sup>28</sup>. Theories of working memory propose that memorized  
214 items are not equivalent, because only one or a few of them can be in the focus of attention<sup>45</sup>.  
215 Studies in the frontal cortex of monkeys revealed that attended and non-attended items in  
216 working memory are represented as sustained activity patterns<sup>46,47</sup>, whereas the present results  
217 suggest that the hippocampus selectively represents the attended noun. The activity of the  
218 neurons largely vanished during the reading of subsequent words, but the cells became active  
219 again in response to a pronoun referring to the cell's preferred concept. Hypothetically, the  
220 representation could have moved into a different neuronal subspace, as observed during  
221 sequence working memory in monkey prefrontal cortex<sup>46</sup>, but this is unlikely given that there  
222 were epochs in which we could no longer decode it from the population of neurons. The activity  
223 profile rather suggests that hippocampal neurons predominantly represent concepts which  
224 come in the focus of attention as a central topic of the narrative. These attended concepts could

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225 then be used for the retrieval of additional associations, a process to which the hippocampus  
226 contributes<sup>48</sup>,

227 In our experiment, pronoun disambiguation was based on gender alone, but in other  
228 sentence constructions, syntax plays an essential role. For instance, in the sentence “The fact  
229 that he is so rich pleases John”, the pronoun “he” can refer to John, but in “He is so rich that  
230 John is pleased”, it cannot. How brain networks implement such syntactic computations is a  
231 topic for future research, which can now be investigated. The present results show how single  
232 unit recordings in the medial temporal lobe contribute to the flexible linkage of words and  
233 concepts during language comprehension.

234

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365 Conceptualization: MWS, PRR, SD

366 Clinical procedures: JCB, SI, PE, RC, VS, IES, SMAS, EA, NCEK, DTR

367 Ethical approval acquisition: MWS, DED, SH

368 Investigation: DED, MWS, JKP, JCP, SH, FR, LK

369 Formal analysis: DED, MWS

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371 Funding acquisition: MWS, PRR

372 Supervision: MWS, PRR

373 Writing – original draft: DED, MWS, PRR

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377

378 **Data availability.** All source data and code to create the main and supplementary data figures

379 will become publicly available via EBRAINS (<https://ebrains.eu/service/share-data/>).

380

381 **Supplementary Materials**

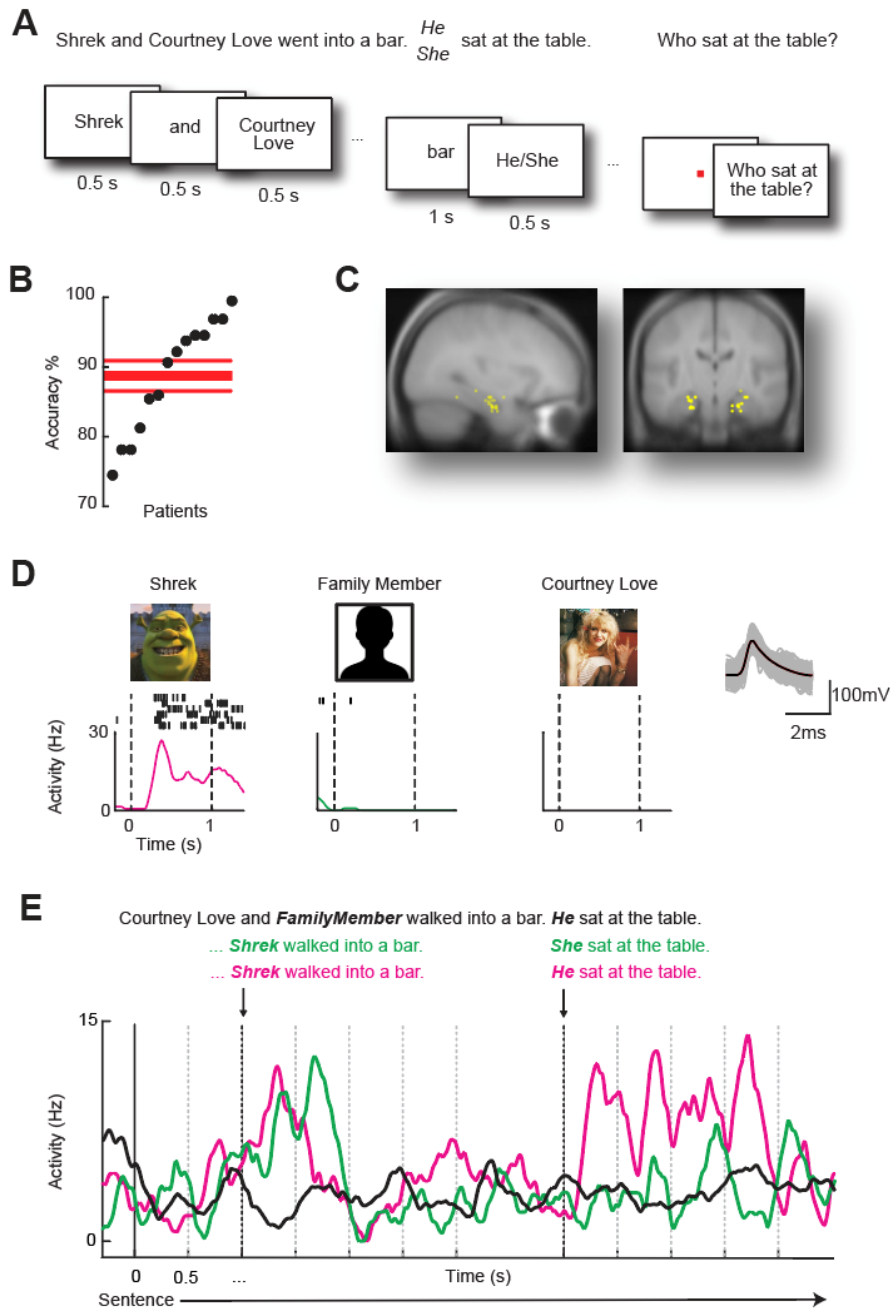
382 Methods

383 Figs. S1 to S5

384 Tables S1 to S3

385

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386

387 **Fig. 1. Reading task.** (A) Two sentences were presented word by word. The first sentence  
388 contained two nouns representing individuals (Table 1 and Table S1). The second sentence  
389 started with a pronoun. The trial ended with a question (see Methods). (B) Accuracy in  
390 answering the question across all patients. Red lines, accuracy  $\pm$  s.e.m. (chance level was 33%,  
391  $N = 14$ ). (C) Locations of the electrodes in the hippocampus. (D) The average response of an  
392 example neuron to different pictures during the screening session, and its waveshape. (E) The

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393 average response of the ‘Shrek’ cell during the reading task. Sentences in which Shrek appeared  
394 as the second noun were followed by a second sentence with the pronoun ‘he’ (magenta) or  
395 ‘she’ (green). Activity on trials in which Shrek did not appear in the first sentence is shown in  
396 black. Black line at time zero, start of first sentence. Dashed grey lines, onset of successive  
397 words. Black dashed lines, presentation of *Shrek* (or the family member) and the pronoun. The  
398 activity elicited by the pronoun was significantly stronger if it referred to Shrek than if it did  
399 not (permutation-based Poisson ANOVA,  $P < 0.001$ ).

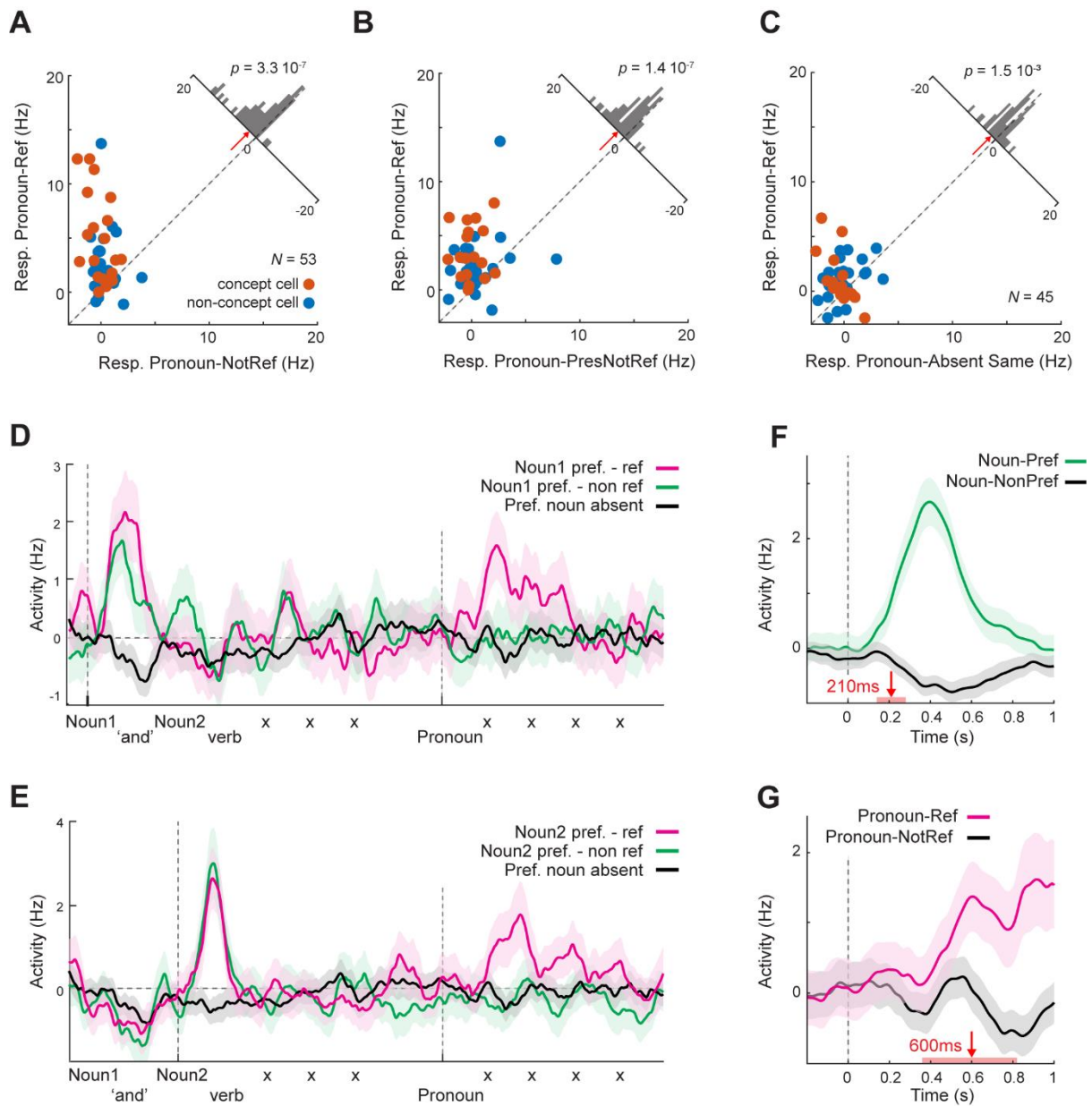
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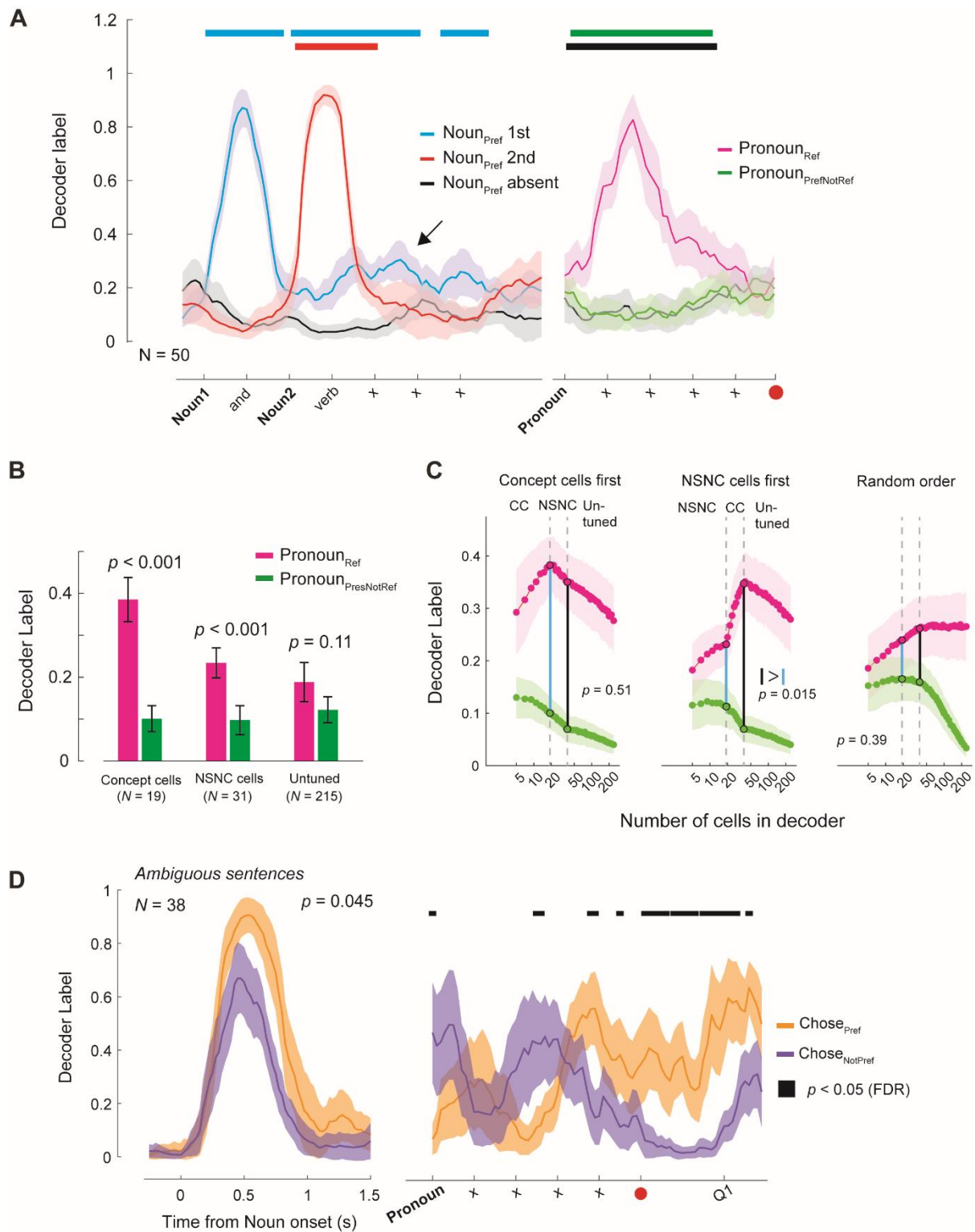
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405 **Fig. 2. Hippocampal responses elicited by nouns and pronouns.** (A) Comparison of activity  
406 elicited by pronouns referring to the preferred noun (Pronoun<sub>Ref</sub>, y-axis) and all pronouns  
407 referring to another noun (Pronoun<sub>NonRef</sub>, x-axis) for concept cells (red dots) and NSNC cells  
408 (blue dots). The inset shows the response difference. Red arrow, median. P-value refers to a  
409 two-tailed paired t-test ( $N = 53$ ,  $t = 5.85$ ,  $p = 3.3 \cdot 10^{-7}$ ). (B) Response to Pronoun<sub>Ref</sub> (y-axis) and  
410 pronouns referring to the other, non-preferred noun on trials in which Noun<sub>Pref</sub> was present in  
411 the first sentence (Pronoun<sub>PresNotRef</sub>,  $t = 6.09$ ,  $p = 1.4 \cdot 10^{-7}$ ) (C) Response to Pronoun<sub>Ref</sub> and the  
412 same pronoun on trials in which the preferred noun was absent from the first sentence

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413 (Pronoun<sub>AbsentSame</sub>,  $t = 3.39$ ,  $p = 1.5 \cdot 10^{-3}$ ). **(D)** Average activity on trials in which Noun<sub>Pref</sub> was  
414 the first noun of the first sentence (Noun1, magenta and green traces) or was absent (black  
415 trace), followed by Pronoun<sub>Ref</sub> (magenta) or Pronoun<sub>PresNotRef</sub> (green). Shading denotes s.e.m.  
416 The vertical dashed lines indicate Noun1 and pronoun onset. **(E)** Average activity on trials in  
417 which Noun<sub>Pref</sub> was the second noun in the first sentence. **(F)** Average activity elicited by  
418 Noun<sub>Pref</sub> and Noun<sub>NonPref</sub>. The red arrows indicate the latency of the response and the red bars  
419 the 95%-confidence interval (determined with bootstrapping). **(G)** Average responses elicited  
420 by Pronoun<sub>Ref</sub> and Pronoun<sub>NotRef</sub>.

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421

422 **Fig. 3. Decoders for the preferred noun.** (A) SVM classifiers trained to distinguish between  
 423 the responses to preferred and non-preferred nouns. The output (y-axis) represents the fraction  
 424 of trials in which the pattern of activity in a time-window is classified as evoked by Noun<sub>Pref</sub>.  
 425 The classifiers were trained on the activity of 50 cells in the noun time-window and then tested

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426 on the two sentences in a series of sliding windows of 0.5s duration. The words are marked at  
427 the centre of the sliding window, the red dot indicates the end of the second sentence. The  
428 shading around the traces indicates the standard deviation across surrogate populations ( $N =$   
429 1,000). Filled bars indicate significant time windows (z-test,  $P < 0.05$ , FDR corrected; see  
430 Methods). **(B)** Decoder output for different cell populations (0.5-1.5 seconds after pronoun  
431 onset) for Pronoun<sub>Ref</sub> (magenta) and Pronoun<sub>PresNotRef</sub> (green). Error bars, standard deviation  
432 across surrogate populations. P-values, z-test on the difference between conditions. **(C)**  
433 Classifier output as function of the number of included units. **Left**, We first added concept cells  
434 (CC:  $N = 19$ ), then NSNC cells ( $N = 19$  cells selected from a total of 31 cells) and then untuned  
435 units ( $N = 215$ ). Decoder output is shown for Pronoun<sub>Ref</sub> (magenta) and Pronoun<sub>PresNotRef</sub>  
436 (green). **Middle**, We first added 19 NSNC cells, then 19 CC cells and then the untuned units.  
437 **Right**, We added units in a random order. We compared the decoder output between decoders  
438 with only CCs, only NSNCs ( $N = 19$ , length of blue vertical lines) to that when cells of the  
439 other category were added ( $N = 38$ , length of black lines) with a z-test to determine significance  
440 (P-values in the panels). **(D)** Decoder output on ambiguous trials. The decoders, which had  
441 been trained on non-ambiguous trials to discriminate between preferred and non-preferred  
442 nouns, were tested on ambiguous trials with two nouns of the same gender. The left panel  
443 shows the decoder output to the preferred noun in the first sentence (aligned on Noun<sub>Ref</sub> onset).  
444 The right panel shows the decoder output during the second sentence, in sliding windows with  
445 a duration of 0.5s. We sorted the trials based on whether the participant selected the preferred  
446 noun (Chose<sub>Ref</sub>, orange) or the non-preferred noun of the same gender (Chose<sub>NotRef</sub>, purple) in  
447 response to the question. Q1, onset of the question.

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Contexts	First sentences:	Second sentences:
English	<i>Noun</i> <sub>1</sub> and <i>noun</i> <sub>2</sub> walked into the bar	<i>Pronoun</i> sat at the table
	<i>Noun</i> <sub>1</sub> and <i>noun</i> <sub>2</sub> sat in the park	<i>Pronoun</i> put some sunglasses on
	<i>Noun</i> <sub>1</sub> and <i>noun</i> <sub>2</sub> were watching the TV	<i>Pronoun</i> suddenly changed the channel
	<i>Noun</i> <sub>1</sub> and <i>noun</i> <sub>2</sub> were having dinner	<i>Pronoun</i> poured out some wine

450 **Table 1. Four different contexts in which the noun and pronouns were used for English**  
 451 **patients.**

452

Condition description	Nouns in the first sentence	Pronoun in the second sentence	Number of repeats*
The first sentence contains the preferred noun and a noun of the opposite gender. The pronoun refers to the preferred noun.	Noun <sub>Pref</sub> + Noun <sub>NonPref</sub>	Pronoun <sub>Ref</sub>	16
The first sentence contains the preferred noun and a noun of the opposite gender. The pronoun refers to the noun with the opposite gender.	Noun <sub>Pref</sub> + Noun <sub>NonPref</sub>	Pronoun <sub>PresNotRef</sub>	16
The preferred noun is not present in the first sentence. A noun of the opposite and of the same gender as the preferred noun are present.	Noun <sub>NonPref1</sub> + Noun <sub>NonPref2</sub>	Pronoun <sub>Absent</sub>	32
- The pronoun refers to the Noun with the same gender		Pronoun <sub>AbsentSame</sub>	16
- The pronoun refers to the noun with the opposite gender		Pronoun <sub>AbsentOppo</sub>	16
All trials where the pronoun does not refer to Noun <sub>Pref</sub> . Noun <sub>Pref</sub> can be absent or present.	Noun <sub>Pref</sub> /Noun <sub>NonPref</sub>	Pronoun <sub>NotRef</sub>	48
The first sentence contains the preferred noun and a noun of the same gender. The pronoun is ambiguous.	Noun <sub>Pref</sub> + Noun <sub>NonPrefSameGender</sub>	Chose <sub>Pref</sub> or Chose <sub>NotPref</sub>	16

453 **Table 2. Noun and pronoun conditions.** The trials with Pronoun<sub>Absent</sub> include all trials with  
 454 Pronoun<sub>AbsentSame</sub> and Pronoun<sub>AbsentOppo</sub>. Similarly, the trials with Pronoun<sub>NotRef</sub> include all trials  
 455 with Pronoun<sub>Absent</sub> and Pronoun<sub>PresNotRef</sub>. \*In two sessions of one of the patients (a total of three  
 456 hippocampal neurons) we recorded only half of the number of trials.